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Two new rare species of *Candolleomyces* with pale spores from China

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Abstract

Most species of *Candolleomyces* have brown or dark brown spores. Although pale-spored members are rare in the genus, we frequently collected two such species from many Provinces during our investigations in subtropical China from 2016–2020. As revealed by morphological characterisation and multigene phylogenetic analyses (ITS, LSU, *β-tub* and *tef-1a*), these species, which we have named *C. subcacao* and *C. subminutisporus*, are unique and distinct from known taxa. In addition, a new combination, *C. cladii-marisci*, is proposed on the basis of ITS sequence analysis of the type specimen. Detailed descriptions, colour photos, illustrations and a key to related species are presented.

Keywords

Basidiomycete, new taxon, Psathyrellaceae, phylogenetic analysis, taxonomy

Introduction

On the basis of extensive comparisons of gene sequences and phylogenetic analyses, the historical genus *Psathyrella* (Fr.) Quél. has been split into several genera. One of these genera is *Candolleomyces* D. Wächt. & A. Melzer, which differs from *Psathyrella* s.s. in lacking pleurocystidia (Örstadius et al. 2015; Wächter and Melzer 2020). Approximately 100 taxa (including synonyms and subspecies) without pleurocystidia have been previously described in *Psathyrella* s.l. (Fries 1838; Smith 1972; Kits van Waveren 1985; Örstadius and Kundsen 2012; Battistin et al. 2014); however, many of these taxa

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have been treated as synonyms, as unique features, based on conventional methods, are scarce (Galland et al. 1979; Kits van Waveren 1980; Knudsen and Vesterholt 2012). Currently, 26 species have been assigned to *Candolleomyces* (Wächter & Melzer, 2020).

According to the research of Wächter and Melzer (2020), *Candolleomyces* may be more speciose than previously thought and better delimitation of species boundaries is needed. Although controversies still exist regarding some species boundaries, the number of new taxa is steadily increasing (Melzer et al. 2018; Sicoli et al. 2019a; Büttner et al. 2020). This continuous discovery of new taxa with clear boundaries deepens understanding of the species in this genus.

Approximately eight taxa in the genus *Candolleomyces* have previously been reported from China (Yan 2018). During our investigations in subtropical China from 2016–2020, we frequently collected two unknown *Candolleomyces* species with pale spores from many Provinces. Spores that are pale or almost colourless in water and 5% potassium hydroxide (KOH) are very rare in this genus. On the basis of our morphological and phylogenetic analyses, the specimens are described as new species in this paper.

Materials and methods

Morphological studies

Specimens were deposited in the Herbarium of Mycology, Jilin Agricultural University (**HMJAU**) and the Herbarium of Fungi, Jiangxi Agricultural University (**HFJAU**). Macromorphological characters and habitat details were recorded from fresh basidiomata. Colour codes were based on the Methuen Handbook of Colour (Kornerup and Wanscher 1978). More than 30 spores, cystidia and basidia in water and 5% aqueous KOH were measured under a microscope. In subsequent descriptions, measurements are shown as (*a*)*b*–*c*(*d*), where *a* is the lowest value, *b*–*c* encompasses at least 90% of values and *d* is the highest value, while *Q* is the length–width ratio of a spore (Bas 1969; Yu et al. 2020).

DNA extraction and sequencing

DNA was extracted from dried specimens using a NuClean Plant Genomic DNA kit (CWBIO, China). Four DNA regions (ITS, LSU, *Tef-1a* and *β-tub*) were selected for analysis (Örstadius et al. 2015) and were respectively amplified using the primer pairs ITS1/ITS4 (White et al. 1990), LR0R/LR7 (Hopple and Vilgalys 1999), EF983F/EF2218R (Örstadius et al. 2015) and B36f/B12r (Nagy et al. 2011). PCR amplifications were performed using the following touchdown programme: 5 min at 95 °C, followed by 15 rounds of 1 min at 95 °C, 30 s at 65 °C (lowered by 1 °C per cycle) and 1 min at 72 °C, followed by 20 rounds of 1 min at 95 °C, 30 s at 50 °C and 1 min at 72 °C, with a final extension of 10 min at 72 °C (Yan and Bau 2018b). Sequencing was carried out by Qing Ke Biotechnology Co. (Wuhan, China).

Table 1. Sequences used in this study.

Taxa	Voucher	Locality	ITS	LSU	*β-Tub*	*tef-1α*
Candolleomyces albipes	DED8340	Sao Tome	KX017209	–	–	–
C. aberdarensis	GLM-F116094	Kenya	MH880928	–	–	–
C. badhyzensis	79478 (TAA) Type	Turkmenistan	KC992883	KC992883	–	–
C. badiophyllus	SZMC-NL-2347	–	FN430699	FM876268	FN396261	FM897252
C. cacao	SFSU DED 8339	Sao Tome	NR148106	–	–	–
	FP1R4	USA	KU847452	–	–	–
	MP2R2	USA	KU847436	–	–	–
C. candolleanus	LAS73030 Neotype	Sweden	KM030175	KM030175	–	–
C. efflorescens	Pegler2133 (K)	Sri Lanka	KC992941	–	–	–
C. eurysporus	GLM-F126263 Type	Germany	MT651560	MT651560	–	–
C. leucotephrus	LÖ138-01 (UPS)	Sweden	KC992885	KC992885	KJ664865	KJ732775
C. luteopallidus	Sharp20863 (MICH) Type	USA	KC992884	KC992884	–	–
	HMJAU5148	China: Jilin	MG734736	**MW301084**	**MW314056**	**MW314073**
C. secotioides	UES2918 Type	Mexico	KR003281	KR003282	–	KR003283
C. singeri	HMJUA37867	China: Jilin	MG734718	**MW301088**	**MW314059**	**MW314077**
	HMJAU37877	China: Chongqing	**MW301073**	**MW301091**	**MW314062**	**MW314080**
Candolleomyces sp.	BAB-4773	India	KP686450	–	–	–
	BAB-5172	India	KR349656	–	–	–
	BAB-4748	India	KR154977	–	–	–
	BAB-4747	India	KR154976	–	–	–
	BAB-5202	India	KT188611	–	–	–
C. subcacao	HMJAU37807 Type	China: Henan	**MW301064**	**MW301092**	**MW314063**	**MW314081**
	HMJAU37808	China: Henan	**MW301065**	**MW301093**	**MW314064**	**MW314082**
	HFJAU1014	China: Jiangxi	**MW559218**	–	–	–
	HFJAU1274	China: Jiangxi	**MW559219**	–	–	–
	HFJAU1488	China:Anhui	**MW559220**	–	–	–
C. subminutisporus	HMJAU37801 Type	China: Hubei	**MW301066**	**MW301094**	**MW314065**	**MW314083**
	HMJAU37916	China: Henan	**MW301067**	**MW301095**	**MW314066**	**MW314084**
C. subsingeri	HMJAU37811 Type	China: Jilin	MG734715	**MW301097**	**MW314067**	**MW314085**
	HMJAU37913	China: Jilin	MG734725	**MW301098**	**MW314068**	**MW314086**
C. sulcatotuberculosus	GB:LO55-12	–	KJ138422	KJ138422	–	–
	HFJAU1515	China: Fujian	**MW375696**	–	**MW382967**	**MW382965**
	Chiarello 07-10-2013	–	KJ138423	–	–	–
C. trinitatensis	TL9035 (C)	Ecuador	KC992882	KC992882	KJ664863	–
	ADK4162 (BR)	Togo	KC992886	KC992886	–	–
Psathyrella cladii-marisci	CLUF302 Type	Italy	MK080112			
Outgroup						
Psathyrella multipedata	LÖ237-04	Sweden	KC992888	KC992888	KJ664867	KJ732777

Note: Newly-generated sequences are in bold.

Data analyses

Taking into consideration the results of BLAST searching against GenBank and the research of Büttner et al. (2020) and Wächter and Melzer (2020), we analysed ITS, LSU, *tef-1a* (Tef 1st, Tef 2nd and Tef 3rd) and *β-tub* (Tub 1st and Tub 2nd) sequences from 37 taxa. Details are presented in Table 1. Sequences were aligned using the online version of the multiple sequence alignment programme MAFFT v.7 (Katoh and Standley 2013), followed by manual adjustment in BIOEDIT v.7.1.3.0 (Hall 1999). Phylogenetic analyses were conducted using Bayesian Inference (BI) in MrBayes v.3.2.6 (Ronquist et al. 2012) and by Maximum Likelihood (ML) in IQTREE v.1.5.6 (Nguyen et al. 2014). For the BI analyses, four Monte Carlo Markov chains were run

for 10 million generations, with sampling every 100th generation and with the first 25% of trees discarded as burn-in (Ronquist et al. 2012). ML analyses were undertaken by applying the ultrafast bootstrap approximation with 1000 replicates. The sequence alignment has been deposited in TreeBASE (S28074).

Results

According to a BLAST analysis, the ITS sequence of *C. subcacao* is 98% similar (eight different loci) to that of *C. cacao* (Desjardin & B.A. Perry) D. Wächt. & A. Melzer and approximately 97% similar (19 different loci) to five ITS sequences from two unnamed species (KP686450 for BAB-4773, KR349656 for BAB-5172, KR154977 for BAB-4748, KR154976 for BAB-4747 and KT188611 for BAB-5202) isolated from *Oeceoclades maculata* (Lindley) Lindley (Bayman et al. 2016). The ITS sequence of *C. subminutisporus* shares 97% similarity (22 different loci) with that of *C. sulcatotuberculosus* (J. Favre) D. Wächt. & A. Melzer. The generated BI and ML trees are shown in Fig. 1 and Suppl. material 1, respectively. In both trees, sequences of the two new species comprise strongly supported clades that are distinct from closely-related taxa. The *C. subcacao* clade groups together with *C. cacao* and two unnamed species with high statistical support, while the *C. subminutisporus* clade clusters with *C. singeri* (A.H. Sm.) D. Wächt. & A. Melzer and *C. sulcatotuberculosus*. The type sequence of *Psathyrella cladii-marisci* Sicoli, N.G. Passal., De Giuseppe, Palermo & Pellegrino is clearly nested within *Candolleomyces*, where it groups most closely, although with only weak to moderate support, with *C. badhyzensis* (Kalamees) D. Wächt. & A. Melzer, *C. badiophyllus* (Romagn.) D. Wächt. & A. Melzer and *C. candolleanus* (Fr.) D. Wächt. & A. Melzer.

Taxonomy

Candolleomyces subcacao **T. Bau & J.Q. Yan, sp. nov.**
MycoBank No: 839231
Fig. 2

Holotype. China. Henan Province: Bird Island, Nanwan Lake, Xinyang City, 32°06'43.32"N, 113°06'03.06"E, 124 m elevation, 17 July 2016, Tolgor Bau, Jun-Qing Yan, HMJAU37807 (holotype!)

Etymology. Referring to its morphological similarity to *C. cacao*.

Diagnosis. Differs from *C. cacao* in having a distinct spore germ pore.

Description. Pileus 11–35 mm, spreading hemispherically to planar, hygrophanous, brown (7E7–7E8), striate up to halfway from the margin or indistinct, becoming slightly dirty white (7B1–7B2) upon drying. Veil pale brown (7A5–7B6), thin, fibrillose, falling off easily. Context thin and very fragile, dirty white (7B1–7B2), approximately 1.0 mm thick at the centre. Lamellae 3.0–4.0 mm wide, moderately

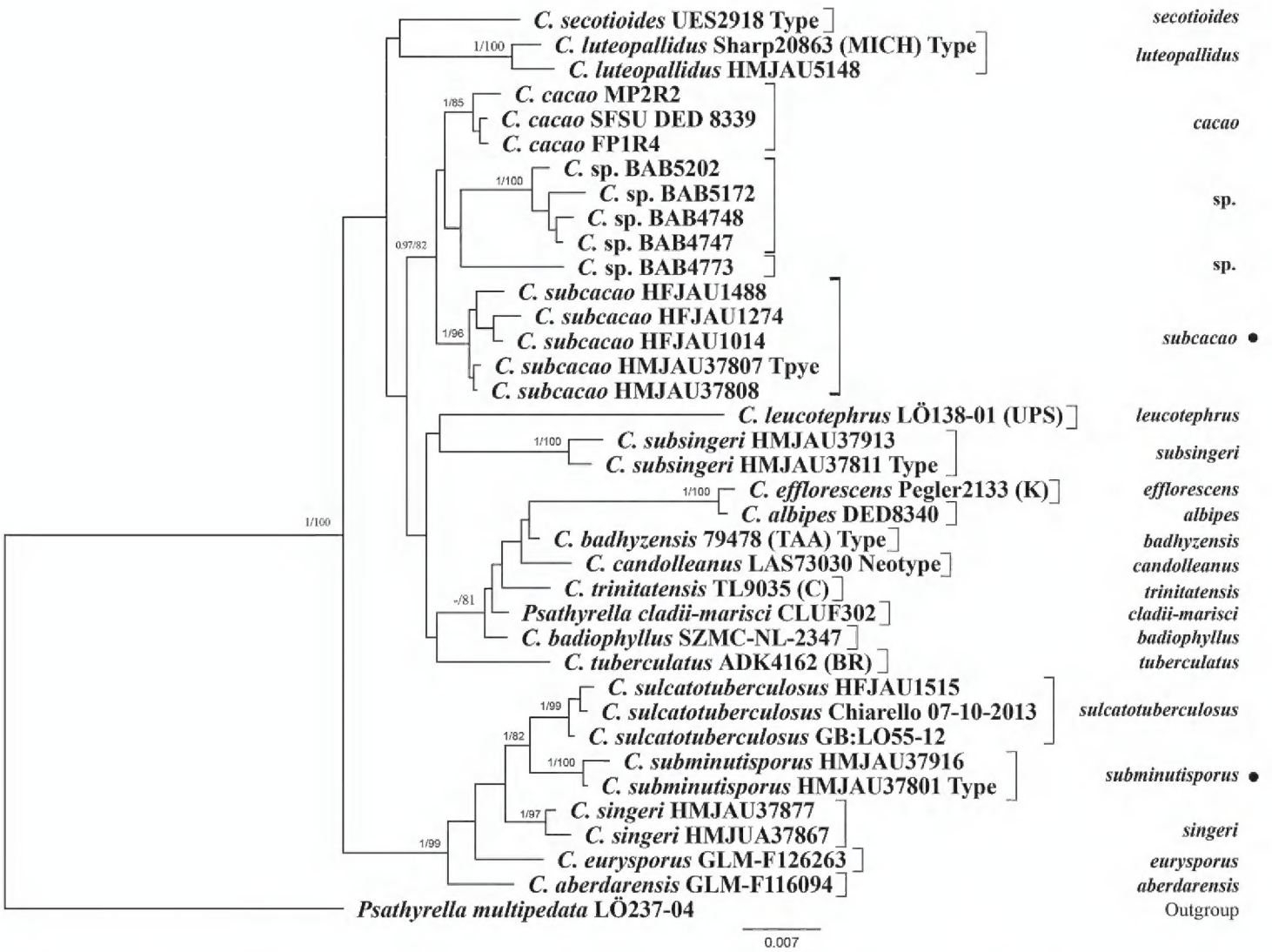

Figure 1. Phylogenetic tree of *Candolleomyces*. The tree was generated by Bayesian analysis of a concatenated dataset of sequences from four nuclear regions (ITS, LSU, *tef-1a* and *β-tub*). *Psathyrella multipedata* (Peck) A.H. Sm. was used as an outgroup. Bayesian posterior probabilities (BI-PP) ³ 0.95 and Maximum Likelihood bootstrap support values (ML) ≥ 75% are shown above nodes as BI-PP/ML. • indicates newly-described species.

close, adnate to slightly adnexed, pale brown (C3–C4) to dark brown (7D6–7E6), saw-toothed under 20× magnification. Stipe 40–50 mm long, approximately 2.0 mm thick, white (7A1–7B1), hollow, equal, smooth, with white fibrils (7A1–7B1) at the base. Odour and taste indistinct.

Spores 6.8–8.0(8.8) × 3.9–4.9 μm, Q = 1.4–1.8, ellipsoid to oblong-ellipsoid, profile slightly flattened on one side, rarely phaseoliform, inamyloid, smooth, pale yellow-brown, darkening in 5% KOH, pale brown, germ pores distinct, but small, approximately 1.0 μm wide. Basidia 17–22 × 6.1–7.3 μm, clavate, hyaline, 4-spored. Pleurocystidia absent. Cheilocystidia 22–36 × 9.8–14 μm, scattered to moderately numerous, various, utriform to fusiform, with an obtuse to broadly obtuse apex, rarely subcapitate or clavate, ovoid, thin-walled. Trama of gills irregular. Pileipellis consisting of 2–3 cells in the deep layer of the subglobose cell, 20–37 μm wide.

Habit and habitat. Solitary to scattered on rotten wood in oak forest.

Other specimens examined. China. Henan Province: Bird Island, Nanwan Lake, Xinyang City, 17 July 2016, Tolgor Bau and Jun-Qing Yan, HMJAU37808, HMJAU37809; Borden Forest Park, Xinyang City, 17 July 2017, Jun-Qing Yan,

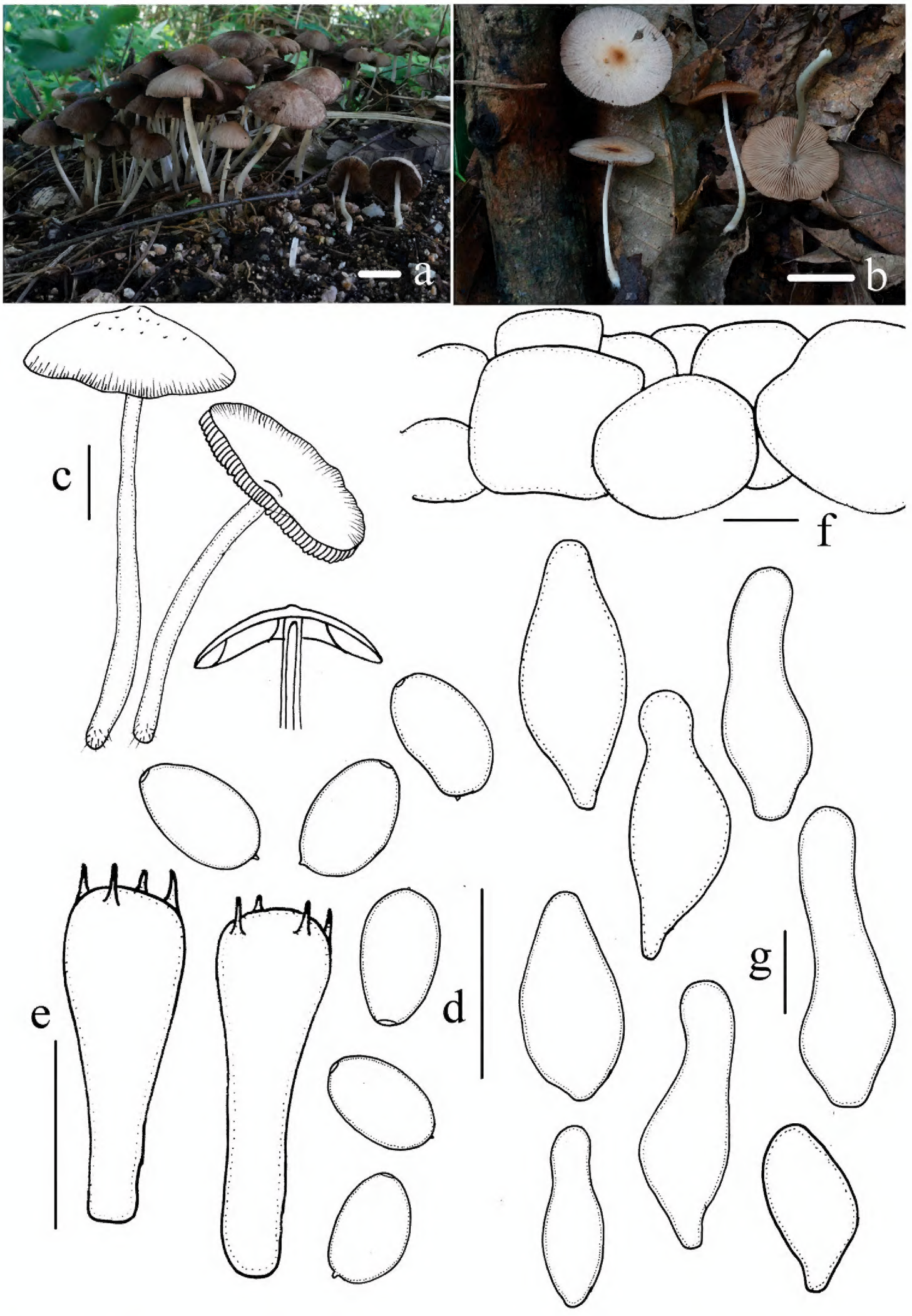

Figure 2. Basidiomata and microscopic features of *Candolleomyces subcacao* **a–c** Basidiomata **d** spores **e** basidia **f** pileipellis **g** cheilocystidia. Scale bars: 10 mm (**a–c**); 10 μm (**d–g**).

HMJAU37898, HMJAU37899, HMJAU37900, HMJAU37948, HMJAU44554; Jiangxi Province: Jiangxi Agricultural University, Nanchang City, 3 June 2019, Jun-Qing Yan, HFJAU0716, 9 June 2019, Jun-Qing Yan, HFJAU1274; Yun Bi Feng National Forest Park, Shangrao City, 5 July 2019, HFJAU1014.

Candolleomyces subminutisporus **T. Bau & J.Q. Yan, sp. nov.**
MycoBank No: 839232
Fig. 3

Etymology. Referring to the small spores.

Holotype. China. Henan Province: Boerdeng National Forest Park, Xinyang City, 16 July 2017, Tolgor Bau and Jun-Qing Yan, HMJAU37801 (holotype!).

Diagnosis. Differs from *C. sulcatotuberculosus* in having smaller spores (5.8–6.8 μm long).

Description. Pileus 8.0–22 mm, spreading hemispherically to broadly conical convex, hygrophanous, pale yellow-brown (6C7–6C8) at the centre, pale at the margin (6A2–6A4), striate from margin to centre, becoming pale brown (6B6–6B7) when dry. Veil present in early stages, thin, white (6A1), fibrillose, evanescent. Context thin and very fragile, 1.0–1.5 mm thick at the centre, same colour as the pileus. Lamellae 2.5–3.0 mm wide, adnate, moderately close, white (6B1) to pale coffee (6B2–6B3), edges saw-toothed under 20× magnification. Stipes 15–40 mm long, 1.0–2.0 mm thick, cylindrical, hollow, white (6B1), sometimes subhyaline or slightly yellow-brown (6A2–6B2) at the base, apex pruinose, evanescent, slightly expanded at the base. Odour and taste indistinct.

Spores 5.8–6.8(7.8) × 3.8–4.9 μm, Q = 1.4–1.8, ovoid, ellipsoid to oblong-ellipsoid, in profile flattened on one side, rarely phaseoliform, inamyloid, smooth, very pale, nearly hyaline in water and 5% KOH, germ pore absent. Basidia 14–20 × 7.3–7.8 μm, 4-spored, clavate, hyaline. Pleurocystidia absent. Cheilocystidia 20–32 × 11–17 μm, utriform, with obtuse apex, bottom side tapering to the long or short stipe. Caulocystidia 27–42 × 6.1–9.8 μm, present at the apex, mostly solitary, various, similar to cheilocystidia or clavate and subcapitate or not. Trama of gills irregular. Pileipellis consists of 1–2 cells in a deep layer of the subglobose cell, up to 36 μm broad.

Habit and habitat. Scattered on rotten wood or humus in *Pinus massoniana* and oak forests.

Other specimens examined. China. Anhui Province: Huangshan City, 3 July 2018, Jun-Qing Yan, HFJAU1253, HFJAU1361; Guangxi Zhuang Autonomous Region: Qingxiushan National Forest Park, Nanning City, 12 Aug 2016, HMJAU37930; Phoenix Valley Forest Park, Nanning City, 17 Aug 2016, Jun-Qing Yan, HMJAU37950; Henan Province: Boerdeng National Forest Park, Xinyang City, 16 July 2017, Jun-Qing Yan, HMJAU37916, HMJAU37958; 17 July 2017, Jun-Qing Yan, HMJAU37959, HMJAU37960, HMJAU37961: Hubei Province: Dagui Temple National Forest Park,

Figure 3. Basidiomata and microscopic features of *Candolleomyces subminutisporus* **a–c** Basidiomata **d** spores **e** basidia **f** pileipellis **g** cheilocystidia **h** caulocystidia. Scale bars: 10 mm (**a–c**); 10 μm (**d–h**).

Suizhou City, 16 July 2016, Tolgor Bau and Jun-Qing Yan, HMJAU37800; Jiangxi Province: Lushan Mountain, Jiujiang City, 30 June 2020, Jun-Qing Yan, HFJAU0921; Yunnan Province: Kunming Botanical Garden, Kunming City, 6 Aug 2016, Jun-Qing Yan, HMJAU37929.

New combination

***Candolleomyces cladii-marisci* (G. Sicoli, N.G. Passalacqua, A.B. De Giuseppe, A.M. Palermo & G. Pellegrino) J.Q. Yan, comb. nov.**
MycoBank No: 839233

Psathyrella cladii-marisci Sicoli, N.G. Passal., De Giuseppe, Palermo & Pellegrino, MycoKeys 52: 99, 2019. Basionym.

Note. According to the ITS phylogenetic analysis including the type specimen, *P. cladii-marisci* belongs to *Candolleomyces* and has a close phylogenetic relationship with *C. candolleanus*, *C. badiophyllus* and *C. trinitatensis*. In addition, the morphological characteristics of this species correspond to *Candolleomyces*, which lack pleurocystidia.

For detailed descriptions and line drawings of this species, see Sicoli et al. (2019a; b).

Discussion

Most species of *Candolleomyces* have dark brown or brown spores, whereas species with pale spores are rare. *Candolleomyces subcacao* is very easily confused with *C. cacao* in the field because of their similar macroscopic characteristics. In addition, these two species have highly similar ITS regions (98%). Nevertheless, some members of *Candolleomyces* with high ITS similarity are still treated as separate species on the basis of morphological characters (Sicoli et al. 2019a; Büttner et al. 2020; Wächter and Melzer 2020). *Candolleomyces subcacao* and *C. cacao* group together, but comprise independent lineages, in the phylogenetic tree (Fig. 1). Moreover, *C. cacao* has ventricose to broad lageniform cheilocystidia, an indistinct germ pore in 5% KOH and a tropical distribution (Desjardin 2016).

On the basis of morphology, *C. subcacao* has been classified into *Psathyrella* sect. *Spintrigerae* using the classification system of Kits van Waveren (1985; 1987) and *Psathyrella* sect. *Subatratae,* based on the system of Smith (1972). Some species in these sections lack pleurocystidia and may thus actually belong to *Candolleomyces*, but molecular analyses of type materials are needed prior to their possible reassignment. In this paper, we have, therefore, only compared these species and the new ones with respect to morphology (see the key below). In particular, two species in these sections possess the combined characteristics of small basidiomata, a pale brown and evanescent veil and pale yellow-brown spores with a distinct germ pore: *P. lacuum* Huijsman, which can be distinguished from *C. subcacao* by the presence of a veil with dispersed white arachnoid fibrils or flocci, abundant pyriform cells at the marginal of the lamellae and very rare utriform cheilocystidia (Kits van Waveren 1985; Battistin et al. 2014) and *P. cordobaensis* A.H. Sm., which differs mainly in having a 10 mm wide pileus, an indistinct germ pore and saccate to ellipsoid cheilocystidia (Smith 1972; Desjardin 2016).

Candolleomyces subminutisporus is characterised by the presence of small basidiomata, a pileus that is striate from the margin up to the centre and very pale to nearly hyaline spores that are mainly less than 7.0 μm long. *Candolleomyces sulcatotuberculo-*

sus and *C. subminutisporus* are morphologically very similar and are phylogenetically closely related (Fig. 1); however, the former has a sulcate-tuberculose pileus surface and much larger spores, which measure (7.6)7.9–8.5(9) × (4.5)4.6–5.0(5.2) μm (Einhellinger 1976). Although Kits van Waveren (1985) and Battistini (2014) detected some smaller spores in these species, which measured (6.2)6.9–7.8(8.9) × (3.6)4.1–4.7(5.0) μm, most spores of *C. sulcatotuberculosus* are clearly longer than 7.0 μm.

Candolleomyces singeri (A.H. Sm.) D. Wächt. & A. Melzer, *C. eurysporus* A. Karich, E. Büttner & R. Ullrich and *C. aberdarensis* (A. Melzer, Kimani & R. Ullrich) D. Wächt. & A. Melzer group together with *C. subminutisporus* in the phylogenetic tree (Fig. 1). These species can be separated as follows: *C. singeri* has larger spores, mostly 6.8–7.8 μm long (Smith 1972, pers. obs. of HMJUA37867 by JQ Yan), whereas *C. eurysporus* can be separated on the basis of its broader spores, a *Q*-value of 1.2–1.6(–1.7) and brown lamellae at maturity (Büttner et al. 2020) and *C. aberdarensis* is distinguished by having larger spores [7.5–8(–8.8) μm long] (Melzer et al. 2018). In addition, two species are morphologically similar to *C. subminutisporus* in having more-or-less pale spores, germ pores that are indistinct or lacking and no pleurocystidia. These species can be separated from *C. subminutisporus* as follows: *C. halophilus* (Esteve-Rav. & Enderle) D. Wächt. & A. Melzer has larger spores, which are 8.6–11 × 4.8–6.2 μm (Esteve-Raventós and Enderle 1992; Battistin et al. 2014) and *C. subsingeri* (T. Bau & J.Q. Yan) D. Wächt. & A. Melzer is easily distinguished on the basis of its stout basidiomata (Yan and Bau 2018a).

Finally, *P. cladii-marisci* was described by Sicoli et. al. (2019) and is characterised by the absence of pleurocystidia and the presence of large spores up to 11 μm long (Sicoli et al. 2019a; b). According to our phylogenetic analysis, this species is relatively closely related to *C. candolleanus*, *C. badiophyllus* and *C. trinitatensis* and should be moved to *Candolleomyces*. A new combination is thus proposed.

Key to related species

1	Spores very pale, nearly hyaline in 5% KOH	**2**
–	Spores pale yellow-brown, greyish-brown or darker	7
2	Spores mostly less than 7.0 μm	**3**
–	Spores up to 8.0 μm	**4**
3	Spores broader, *Q* = 1.2–1.6, lamellae brown at maturity	***C. eurysporus***
–	Spores slenderer, *Q* = 1.4–1.8, lamellae pale coffee at maturity	***C. subminutisporus***
4	Surface of pileus is sulcate-tuberculose, up to two-thirds of the radius	***C. sulcatotuberculosus***
–	Not as above	**5**
5	Pileus less than 10 mm wide, lamellae brown	***C. aberdarensis***
–	Not as above	**6**
6	Basidiomata stout, spores up to 5.5 μm broad	**C. singeri**
–	Basidiomata slender, spores up to 4.5 μm broad	***C. subsingeri***
7	Spores up to 11 μm, growing on plant debris in brackish water	***C. halophilus***
–	Not as above	**8**

8	Germ pore distinct	**9**
–	Germ pore indistinct	**10**
9	Margin of lamellae with abundant pyriform cells, utriform cheilocystidia very rare	***P. lacuum***
–	Not as above	***C. subcacao***
10	Cheilocystidia ventricose to broadly lageniform	***C. cacao***
–	Cheilocystidia saccate to ellipsoid	***P. cordobaensis***

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Supplementary material 1

Phylogram generated by Maximum Likelihood (ML) analysis

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Data type: phylogenetic tree

Explanation note: Phylogram generated by Maximum Likelihood (ML) analysis of *Candolleomyces* based on sequences of a concatenated data set from four nuclear regions (ITS, LSU, *Tef-1a* and *β-tub*), rooted with *Psathyrella multipedata* (Peck) A.H. Sm. (/multipedata clade). ML bootstrap proportion (ML-BP)≥ 75% are shown. ● indicates newly described species.

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